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The stem of Ibervillea Sonorae*

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(WITH PLATE 24)

Among the representatives of the *Cucurbitaceae* at the New York Botanical Garden is a group of plants of *Ibervillea Sonorae.* They were brought from the southwest by Dr. D. T. MacDougal in 1902, and are interesting because of their unusual character for cucurbits as well as for their adaptation to desert conditions. A description of the plants is given by Miss J. T. Emerson collaborating with Mr. W. W. Welker in a paper, in coarse of preparation, on its chemistry and pharmacology (34). FIGURES A and B show the organographic characters of the species, both at the adult stage in its native habitat, and as a seedling from four to five years old. The "large projecting root" (21) of *Ibervillea* in the specimens in the greenhouses of the Botanical Garden reaches a diameter of from 25 to 30 cm. In the desert this enormous tuberous growth lying in the dry sand looks like a gray, dust-covered boulder. Frequently irregularities of shape give it still more the effect of stone, and it is only when the cortex is flecked off that one discovers the healthy green color beneath the superficial layer. From the tubers arise yearly long flexible liana-like shoots which reach a length of three or more meters. The shoots are round, smooth and green above, brown-gray and gray-spotted or streaked below. The flowers are dioecious, the tendrils branched, and the leaves bright-green and twice three-cleft as is so frequently the case throughout the family. The fruit is said to

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* A research pursued in the laboratories of Barnard College during the winter of 1904-1 05.

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be "amber-colored" (21) and one and a quarter to one and a half inches long; none has ripened in the greenhouse, as the flowers there are staminate only. The plant is able to persist in its arid habitat with remarkable vitality. In fact, so provident is it of water and nutritive substances that one in the museum case at the Garden which has been lying on a board since 1902 is in 1907 still sending up yearly shoots bearing leaves and tendrils. Every fall the shoots die back and sprout again early the next spring. The Indians of the desert call the plant "Guarequi," and a decoction of its root is much used as a cathartic.

The forms which show perennial growth among the *Cucurbitaceae* are comparatively few in number, and many of them are tropical species or types seldom seen. Of those which have tuberous stems or roots the most familiar are *Thladiantha* and *Bryonia*. The large slices of the *Bryonia* root are well known in pharmacy, and Weiss (10) refers to a root 20 cm. in diameter and 10 kg. in weight. More work has been done on *Bryonia* than on any other perennial form. It was pictured by Jacquin in 1774 as an example of perennial growth, and reference is made to it in most of the papers mentioned below.

The history of *Ibervillea* is given in full by Miss Emerson, so that only the most important citations are noted here. The first species of the genus was described by Gray (1) in 1850, from Texas and Mexico, as *Sicydium Lindheimeri*. In 1881 Cogniaux (11) separated from *Sicydium* the genus *Maximowiczia* Cogn., with three species. The first description of *Maximowiczia Sonorae* was published by Sereno Watson (21) in 1889. It was one of the numbers of the collection of Dr. E. Palmer found in 1887 about Guaymas, Mexico. Not only the range of *M. Sonorae* but that of the entire genus is purely American. As the name *Maximowiczia* had been previously used for another genus, the name *Ibervillea* was given to the present one by Greene (27) in 1895, and the species here discussed named by him as *Ibervillea Sonorae*. The only anatomical study of the genus has been made by Fischer (17), who included it in his thorough general survey of the family. It will be of advantage first to describe the normal structure of the Cucurbitaceous stem. The terminology used is that of Haberlandt (32).

The stems of cucurbits are usually five-angled, and only in exceptional cases seven-angled or terete. A transverse section through a stem of this type, or five-angled stem, exhibits two circles of bundles, five in each circle, the outer standing in the angles, the inner in the furrows. The bundles are normally all bicollateral, possessing an outer leptome, a hadrome region, and an inner leptome. Both inner and outer leptome contain very large and prominent sieve-tubes, as well as much leptome parenchyma. The common opinion seems to be that there is no inner cambium, though the outer cambium is a wide and active zone peripheral to each hadrome strand. The bundles are widely separated, and lie in a large-celled ground parenchyma. The pitted vessels of the hadrome are exceptionally large, and in older stems are braced by thyllae. A continuous ring of stereome borders the outer limit of the pericycle, and there is a row of starch-filled cells, accompanied by various arrangements of chlorophyl-free collenchyma just beneath the epidermis. There are frequently hairs or glands on the epidermis, and sieve-tubes scattered through the cortex and pericycle. Inner secretory passages are wanting, and deposits of calcium carbonate seem to occur only in the leaves. As the stems are mostly annual a periderm does not form, and for the same reason no true bark is found. Many species show a lysigenous cavity in the pith making the stem hollow, and because its secondary growth chokes this cavity and fills it up *Bryonia dioica* is mentioned as peculiar.

In describing *Ibervillea* it will be taken first as a primary stem at the end of the first year, and later as a secondary stem, and a diagram of the transverse section of the young shoot cut 24 cm. from its tip where the stem was fresh and green is given in PLATE 24, FIGURE 1. This shows the general outline of the section to be irregular with a possible tendency toward the seven-angled type, though its external appearance is smooth, the number of the blunt "angles" varies, and as it grows older it is always terete. The bundles are arranged in two rings, those of the outer being smaller. The number of those in the inner ring is always five, that of the outer ring varies from five to seven or even nine. An attempt is at once suggested to place the stem in one of the classes made by Lotar (12), Petersen (14), or Tondera (31). Different numbers of bundles are given by these authors for the same form, but in *Ibervillea*, as Weiss (15) found to be the case, the number may vary not only in the same species and the same plant, but even in the same internode. In a well-developed branching stem with a length of 310.6 cm. there were at the base ten bundles, at the first fork twelve bundles in each branch, thirteen in the main branch above, and in its side shoots most frequently twelve, but sometimes thirteen or fourteen. Lotar (12), too, says that differences may occur, due to the temporary splitting of individual bundles.

In the single growing tip which my material afforded there were eleven procambial strands, so that the number is not derived from a primitive procambial ten, but doubtless varies in the separation of the young meristems. The structure of the bundle is altogether normal. The well-formed hadrome, which is cut off centrifugally by the cambium which lies along its outer surface, shows the usual succession of ring, spiral, and pitted ducts, and the last are very large, and always surrounded by wood-parenchyma. The outer leptome contains large sieve-tubes with prominent sieve-plates and companion-cells; there is also much leptome-parenchyma and the outer and inner leptome are alike in their constituent elements. The outer cambium region consists of several rows of brick-shaped cells, while the inner or medullary cambium (FIGURE 10) shows cells more polygonal in outline, and is more localized in its later divisions.

The ground-tissue in *Ibervillea* is always solid, consisting of large parenchyma-cells of which the walls are more and more conspicuously pitted as the stems grow older. The cells are ordinarily full of starch which occurs in large grains crowded together so densely that the tissues of the bundles stand out in sharp contrast. Several rows of large cells intervene between the bundles and the stereome-ring. The latter (FIGURE 2, *st*) is from two to three cells wide and consists of lignified fibrous cells marked with cross-shaped pits. It breaks up as soon as the stem begins to enlarge, and the dilatation-changes progressively fill up the interstices. Without the stereome-ring is found a row of starch-containing cells (FIGURE 2, *end*) with the radial walls at right angles to the tangential, and slightly more oblong in cross-section than the adjacent parenchyma-cells, which Van Tieghem (13) cites as the endodermis. Outside of the endodermis there are two layers of chlorenchyma with autochthonous starch (FIGURE 2, *ch*), and then two layers of angle-collenchyma (*col*), chlorophyl-free, bordered by a large-celled epidermis. There are occasionally stomata, but they show no special adaptations to desert conditions, nor is the cutin-layer unusually thick.

There remains to be mentioned a system which has been admirably treated by Fischer (17), namely the sieve-tubes which are found scattered singly or in groups throughout the pericycle and the cortex. The discovery of supernumerary sieve-tubes just inside the stereome-ring was made by Sanio (4) in 1864 in *Cucumis sativus*. DeBary (6) found them in the same position in a number of other species, but Fischer added two new categories to those of Sanio and de Bary. To the study of their development and physiology he devotes 109 pages. He finds sieve-tubes with companion-cells and "nebencellen" without as well as within the stereome-ring. There are also horizontal series which he designates *commissural* sieve-tubes and sieve-bundles which connect with the leptome of the bundles and with each other. These sieve-tubes are to be seen only in the very young tips, for they function during the period of elongation, and owing to the pressure of the growing tissues about them soon lose their typical structure. Fischer describes their progressive phases of development according to Sachs' phases of growth, and treats especially of the meristematic period of elongation. The first sieve-tubes to appear in the stem, which function before any of the others, lie on the edge of the outer procambial strands between the more typical phloem region and the mother-tissue of the stereome-ring. At this stage the procambial strand borders closely on this mother-tissue, but later by the development of parenchyma they become more isolated from the bundle and stand out in the pericycle. In *Ibervillea* they are very prominent, with large conspicuous sieve-plates.

Following these there appear first the sieve-tubes of the outer leptome, and with them the subepidermal ectocyclic sieve-cells and the ectocyclic cells which are found among the collenchyma. The inner leptome comes next in order, and just before the end of the meristematic elongation the endocyclic sieve-tubes mature. The commissural strands may originate with, but never before, the endocyclic groups. All of these small sieve-bundles without the leptome and such commissural sieve-tubes as serve to connect them with each other are transitory in their activity, and by the end of the elongation-period are obliterated. The obliteration follows the reverse of the order in which they appeared, so that the endocyclic succeed the ectocyclic, and the commissures are the last to lose their identity. Fischer holds that the first sieve-tubes help to distribute the proteid substances to the young tissues of the stereome. Late they are reinforced in their office by the endocyclic sieve-tubes. They develop from the procambial strand, while the endocyclic sieve-tubes are derived partly from the mother-tissue of the stereome and partly from the ground-parenchyma. Ectocyclic sieve-tubes come from the mother-cells of the collenchyma and stereome, and at first support the young collenchyma, which grows rapidly in the early stages. When it has thickened and reached its maturity the outer ectocyclic cells are obliterated. The remaining ectocyclic tubes in the chlorenchyma and all commissural cells come from the secondary meristems derived from the parenchyma-cells of the pericycle and cortex.

The endocyclic sieve-tubes, as indicated above, nourish the developing stereome-ring and when its permanent character is determined they are obliterated. The commissures are obliterated last of all, and the order of their degeneration is one of the strong reasons why Fischer concludes that they serve to withdraw the proteid substance from the endocyclic sieve-tubes and from each other into the leptome of the bundles. The office of the sieve-tubes of the bundles and the course of their obliteration needs no special comment; the development of the procambial strand and the support of the growing cambium is dependent upon their activity. The sieve-tubes outside of the stereome-ring are connected with those inside only at the nodes, so that the endodermis and the mechanical tissue are never broken by the commissures.

The genera of the *Cucurbitaceae* are divided into classes upon the character of the supernumerary bundles, of which *Maximowiczia* (*Ibervillea*) belongs to the *Cyclanthera* type. There are said to be present countless endocyclic sieve-tubes (FIGURE 4) united partly with each other and partly with the vascular bundle by *very few* commissures. The *Ibervillea* at the Garden also possesses

(FIGURE 3) many ectocyclic sieve-tubes, but in only one or two instances has a young commissure appeared. In these cases the length of the members of the sieve-tube was that of the diameter of the mother parenchyma-cell, the two separated by a large, well-formed vertical sieve-plate. The peripheral sieve-tubes are easily seen in the very young stem (FIGURES 3 and 4) while the first tracheal elements are appearing and the sieve-plates are exceedingly delicate and distinct.

The obliteration of the sieve-tubes Fischer treats separately. They sometimes entirely lose their identity, owing to the pressure of the surrounding tissues and the torsions of the stem, but sometimes when the callose breaks down and the contents begin to degenerate, there appears in them a slimy substance giving to the older stem an appearance which leads him to say: "One may see that we have here another category of cell-derivatives, that our commissures and ectocyclic sieve-tubes belong to a hitherto overlooked latex-system," and again he says that the presence of these ramifying cells in the stem produces the effect of an internal secretory system. He takes up this point at length in a later paper (20) and refers to Hanstein's theory of the contents of the obliterated sieve-tubes as "Lebensaftgefässe," where Hanstein assumed that the contents were active while they were in reality hard and gum-like. A section through a stem of *Ibervillea* after its period of elongation is completed (FIGURES 9 and 2) shows inside of the medullary leptome, peripheral to the outer leptome, and through the pericycle and cortex, groups of cells both in structure and position identical with the obliterated sieve-elements. They contain a highly refrangible homogeneous substance of a brownish-yellow color which makes them very conspicuous. They occur ordinarily in pairs, frequently in groups of from three to twelve (FIGURES 5 and 6). The contents color orange with hydrochloric acid and phloroglucin, while the contents of the active sieve-tubes remain lemon-yellow. With Millon's reagent they turn brick-red.

Longitudinal sections frequently show the old sieve-plates, and the companion-cells seem to have contents identical with those of the sieve-tubes. The groups of cells are rarely seen to anastomose in young stems, but they frequently run a tangential or radial course, and may connect within a short distance in this manner. In older stems, especially where they widen toward the tuber, they form an elaborate ramifying system throughout the periphery and the pith, as well as in connection with the supernumerary bundles which then develop (FIGURES 5 and 8). When such stems, perhaps two and a half centimeters in diameter, are cut, the contents of these passages ooze out, forming a large viscid transparent drop which covers the wound and which immediately hardens, forming a variety of wound-gum. When the sieve-tubes retain their content so generally, and when the contents are so evidently secretory in nature, one seems to be justified in calling them a secretory system of the secondary stem, and might take exception to Solereder (28) for saying generally for the entire family " Innere Sekretbehälter fehlen."

The secondary growth in the sense of the growth of a second year is illustrated in FIGURE 9. Its most prominent features are the increase in the size of the bundles and in the amount of leptome and hadrome, the great width of the medullary rays, the breaking of the stereome-ring, and the presence of a prominent periderm entirely surrounding the terete stem. One is also struck by the absence of any appearance of distortion due to the compression of the tissues, as this is true only in the horny regions of the leptome. The increase in the size of the bundles has been effected by the constant activity of both inner and outer cambium.

The amount of leptome produced is enormous. The outer cambium gives rise to all the hadrome elements, vessels, and wood-parenchyma, and by its centrifugal divisions also generates the outer leptome. It consists of a succession of brick-shaped cells which spread across the entire tangential surface of the hadrome. Peripheral to this is the mass of the outer leptome which contains parenchyma and many large conspicuous sieve-plates in the sieve-tubes. The inner leptome is similar to the outer in character, but the cambium is less regularly distributed. It is represented by a group of meristematic cells just within the inner tangential surface of the hadrome (FIGURE 11 c_2). These cells are polygonal in outline and are confined to the middle of the surface. The lines of cells x and y can be traced back to this origin. In many bundles a second series of divisions is localized so as to make a distinct line across the outer surface of the leptome (as in FIGURE 11) with the appearance of a normal cambium. The line does not always show distinctly and is more apt to occur in large bundles.

These conclusions concerning an inner cambium do not agree with those of Bertrand (9), Lotar (12), and Schenck (26), who found hadrome formed by the inner cambium, nor with those of Fischer (17), who remarks the absence of an active inner cambium, saying that for a while the still procambial cells have the appearance of one. It is rather the state of things noted by Vesque (5), who claims as a false cambium one which produces only leptome; and afterward found by Scott and Brebner (25) in *Thladiantha*. The latter authors state that when a cambium is present it produces leptome only.

Around the oldest tangential borders of the leptome-regions are found the horny walls of the disorganized (obliterated) sieve-elements as well as masses of cells filled with yellow-brown gum whose localization is illustrated in FIGURE 9. The breaks in the stereome-ring are filled up with parenchyma, and dilatation-changes also occur in the medullary rays and the pericycle by which they keep pace with the increase in the size of the stem.

It occasionally happens, as Hérail (19) found to be the case in *Ecballium*, that the tangential divisions of the parenchyma may be so localized between two bundles as to give the appearance of an interfascicular cambium. Potter (22) found an interesting interfascicular cambium in *Thladiantha* which connected bundles of the inner and outer circles, showing as de Bary had said that the two concentric rows function as a single ring. New medullary rays are not formed yearly. In large old stems two or perhaps three may occur (FIGURE 13), but this is in very old plants, and they develop only at long intervals. The periderm is superficial in origin. It arises from the layer of the collenchyma just beneath the epidermis. It soon becomes spotted or streaked with deposits of calcium carbonate in the radial and tangential walls of the phellem. The epidermis breaks away over the encrusted areas, and the gray color which appears in the stem is due to the exposure of such groups of cells. When the calcium carbonate is dissolved out with hydrochloric acid, the walls of the cells give the lignin reaction with phloroglucin.

A section at the base of a stem two and a half centimeters in diameter shows a new feature of considerable interest. This is the appearance in the medullary rays of supernumerary leptome-bundles which Pitard (30) calls tertiary bundles, consisting of semicircular meristematic areas of which the long axes of the meristems are parallel with the medullary rays, so that the axis of any bundle is at right angles to that of the primary bundle next to it. The bundles frequently appear to be collateral and contain hadrome elements on the side next the wood of the primary bundles. The phenomenon is one not infrequently found among the *Cucurbitaceae.*

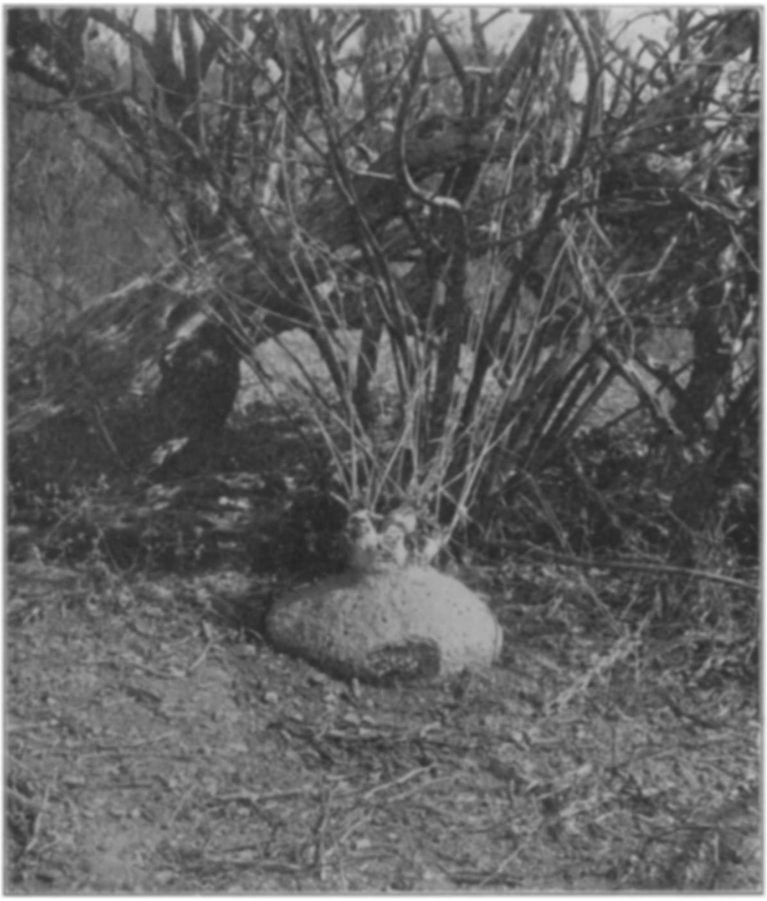

FIGURE A. *Ibervillea Sonorae* in its native habitat.*

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* This photograph was used for *plate 16* of Carnegie Inst. Publ. No. 6.

It is treated by Leisering (29), deBary (6), Morot (18), Hérail (19), VanTieghem (24), and Weiss (15). Weiss pictures such bundles in the root of *Bryonia*, where masses of leptome are found to be associated with hadrome elements. He concludes that tracheae are separated by dilatation-parenchyma from the primary masses of the hadrome, and serve as centers of meristematic division in the ground-parenchyma, while the semicircular meristem gives rise to the leptome. The meristematic parenchyma-cells are said to come originally from the primary cambium. Scott and Brebner (25) describe their work with *Thladiantha*. They find, elaborating Dutailly's treatment of the same form (7), the elements of the hadrome separated out by dilatation-changes, but differ from Weiss in finding that the leptome bears no constant relation to the tracheae, and that it is partly formed directly from the cambium. This work in each case is on the root. In *Ibervillea* the general dilatation extends to the unlignified parenchyma of the hadrome, and of the parenchyma adjacent to the bundle. Such parenchyma lateral to the hadrome begins to divide and sometimes tracheae are "nipped" off by the changes and isolated with the meristematic cell. In either case the formation of new cells in the dilatation pushes the meristem out into the medullary ray. The meristem then produces leptome but never hadrome, and as the stem increases in size the course of the bundles becomes irregular, so that it is often easy to see the sieve-tubes in longitudinal position. FIGURE 12 shows such a meristem in the midst of a starch-filled parenchyma.

One of the characters of the older secondary stems is the anastomosing of the bundles. Both the leptome and the hadrome frequently run a horizontal course from bundle to bundle, so that the center of the stem is a medley of supernumerary sieve-regions and it is impossible to trace any regular arrangement. As a whole the stem retains the character of its first secondary growth. The parenchma of the medullary rays continues to divide tangentially and radially and the increase in pericycle and cortex is through the same sort of change. Minute fragments are all that remain of the stereome-ring, though opposite these one can still trace the old cortical parenchyma. A relatively large production of phelloderm adds most of the soft tissue in the outer part of the periphery of the tuber, and like the ground-parenchyma the walls of all these cells are pitted and very thick. The periderm renews itself constantly and continues to be sloughed off, while the abundant calcium carbonate gives the gray color to the entire surface. There is no true bark, nor are there any deeper-seated phellogens. The course of the bundles has not been investigated. De Bary says that the bundles of the *Cucurbitaceae* are bundles of the leaf-trace running up two internodes. Accounts are given by Bertrand (9) and by Lotar (12), and later by Leisering (29) and by Tondera (31). The latter, by sections and maceration combined, has secured details of the complicated connection at the nodes which he presents in a series of elaborate diagrams.

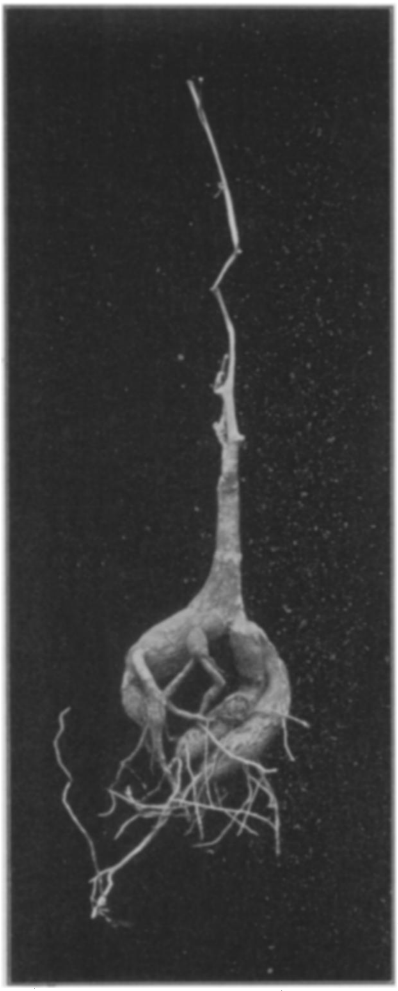

FIGURE B. *Ibervillea Sonorae*, four or five years old.

A reference to the description of *Ibervillea* (21) will remind one that this tuber is ordinarily referred to as a root, and that its closest analogies seem to be the roots of *Bryonia* and *Thladiantha*. The picture of the old plant (FIGURE A), with its shoots rising from the tuber, shows the gradual enlargement of the stem, though the appearance of the seedling (FIGURE B) would indicate that the swollen portion includes root, hypocotyl and stem. As far as this investigation goes the formation is stem, and at least half of the swollen portion may claim that distinction, and as the bases of the shoots are sometimes four and a half centimeters broad one can get intermediate stages between green lianas and tubers. The age of the plants is difficult to estimate. The seedling photographed has been in the greenhouse four years. The shoot in FIGURE 9 is over two years old. The size of the ducts must seemingly be taken as the criterion, and each two or possibly three large tracheae must constitute the growth of a season. There is usually associated with the fall growth the formation of unlignified wood-parenchyma at the side of the hadrome, so that the region presents the jagged appearance noted in FIGURE 13. That the large tubers are fifty years old is doubtless a most conservative estimate.

The pharmaceutical character of the stem is only known empirically to the Indians, who regard it as very poisonous, but more so than has been found to be the case by Miss Emerson and Mr. Welker. The stem shows quantites of starch at the end of the growing season, but the shoots die back so short a distance that it is extremely improbable that the nutritive substances are withdrawn into the tuber. In the desert, the drier condition may effect a change in its habit so that the shoots shrivel further down toward its base. The mechanics of the stem after the breaking up of the stereome-ring are those of a true liana. The plant is not only quick of development in a short rainy season as well as resistant in a dry one, but it is able to twine about surrounding woody growth and to expose a relatively large leaf-surface above the sandy levels. It is perhaps to be noted that the leaves when older have a white spotted appearance, and would doubtless prove to be good material for the study of cystoliths.

The differential characters of the stem may be summed up as follows:

1. The shape is terete, with from ten to fourteen bundles.
2. It possesses endocyclic as well as ectocyclic and commissural sieve-tubes.
3. It has an active inner cambium.
4. The obliteration of the sieve-tubes changes them into a secretory system of which the contents serve as wound-gum.
5. There is a periderm with phellem and phellogen.
6. Deposition of calcium carbonate is abundant.
7. There develop in the secondary stem supernumerary leptome-

bundles formed by meristematic parenchyma of the medullary rays.

8. There is absence of interfascicular cambium and dilatation of all parenchyma.

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Explanation of plate 24

The figures were drawn with Leitz lenses and an Abbé camera-lucida and the magnifications have been reduced two-thirds in reproduction.

Fig. 1. Diagram of transverse section of primary stem. l_1, outer leptome; l_2, inner leptome; *st*, stereome-ring; *h*, hadrome; *x*, bundle pictured in Figure 10. × 414.

Fig. 2. Transverse section of portion of cortex of primary stem. *e*, epidermis; *col*, collenchyma; *ch*, chlorenchyma; *os*, obliterated sieve-tubes; *end*, endodermis; *st*, stereome. × 775.

Figs. 3 and 4. Transverse sections of portions of cortex of young stem. *e*, epidermis; *col*, collenchyma; *st*, stereome; *ec. s*, ectocyclic sieve-tube; *en. s*, endocyclic sieve-tube. × 775.

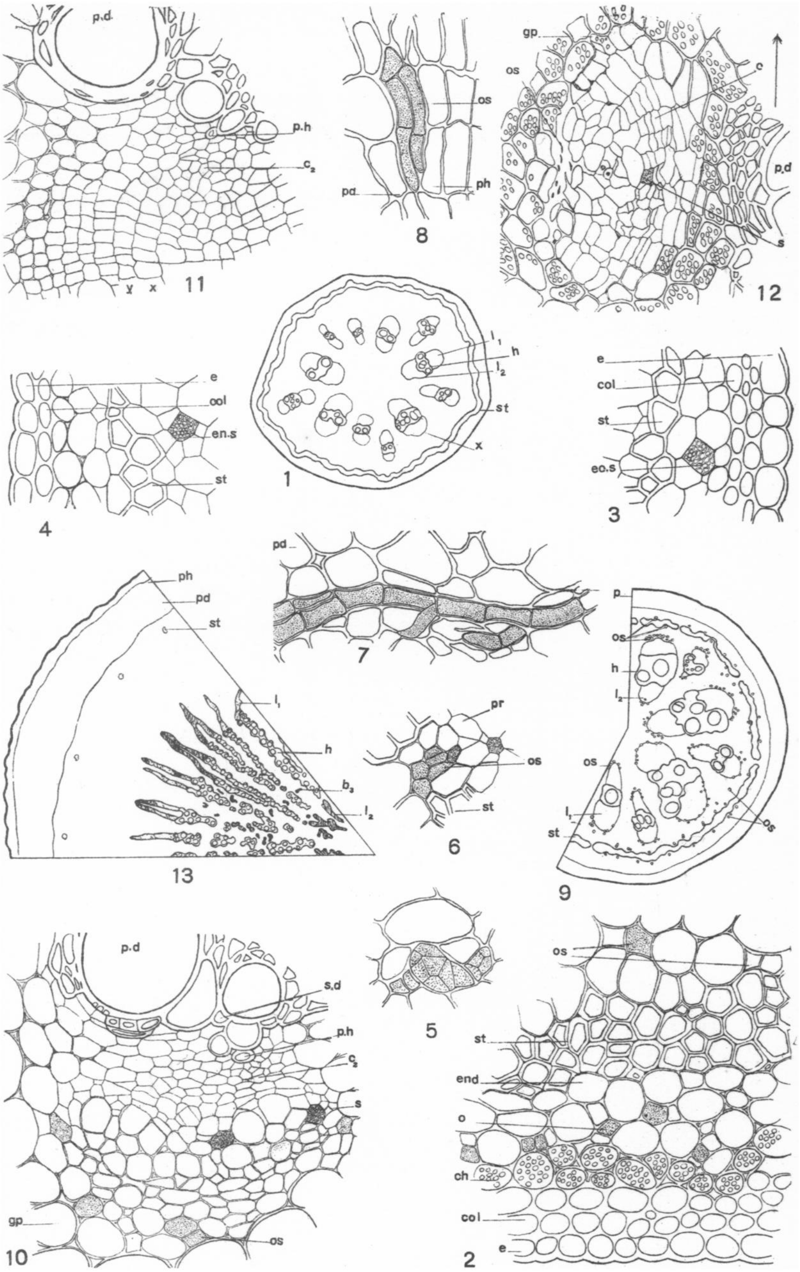
Figs. 5–8. Transverse sections of cortex of stems, showing appearance of groups of obliterated sieve-tubes. *st*, stereome; *pr*, parenchyma; *ph*, phellem; *pd*, phelloderm. Fig. 5, periphery of outer leptome; Figs. 6–8, cortex. × 650.

Fig. 9. Diagram of transverse section of two-year stem. *p*, periderm; *os*, obliterated sieve-tubes; *h*, hadrome; l_1, outer leptome; l_2, inner leptome; *st*, stereome. × 44.

Fig. 10. Transverse section of bundle of inner ring showing inner cambium of a primary stem. Fig. 11 the same on a secondary stem. *p. d*, pitted duct; *s. d*, spiral duct; *p. h*, protohadrome; c_2, inner cambium; *s*, sieve-tube; *os*, obliterated sieve-tube; *gp*, ground-parenchyma. × 480.

Fig. 12. Transverse section of old secondary stem showing tertiary bundle. The arrow shows the direction of the axis of the primary bundle. Lettering as in Figs. 10 and 11.

Fig. 13. Diagram of section of very old stem. Lettering as before; b_3, tertiary bundle. The shaded portions are leptome. × 180.



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